Global Ecology and Conservation 19 (2019) e00657

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Short Communication

Influence of the physical dimension of leaf size measures on the goodness of fit for Taylor's power law using 101 bamboo taxa

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ARTICLE INFO

Article history:
Received 10 April 2019
Received in revised form 7 May 2019
Accepted 7 May 2019

Keywords:
Bamboo
Goodness of fit
Exponent of Taylor's power law
Log-transformation
Mean-variance relationship

ABSTRACT

The mean and variance of ecological measures usually follow a power-law relationship, referred to as Taylor's power law (TPL). Leaves are important organs for photosynthesis, and leaf size is closely related to photosynthetic potential. Leaf size has different physical measures, such as leaf length, area, and fresh or dry weight. However, it has not been reported whether these leaf size measures follow TPL and whether the estimates of the TPL exponent reflect basic topological constraints. Considering that the variation of leaf size can affect the photosynthetic capacity of leaves and plant competitive abilities in communities, we examined the effects of different physical dimensions of leaf size (including leaf length, area, and fresh and dry weight) on the estimate of the scaling exponent and the goodness of fit of TPL for 101 bamboo species, varieties, forms, and cultivars, using 90–100 leaves for each type of plant. All leaf size measures follow TPL. However, the goodness of fit increases with the physical dimension of the leaf size measure (e.g., from 1D leaf length to 3D leaf weight). Interestingly, no significant differences in the estimates of the TPL exponent were detected among any of the physical dimensions (1D to 3D) because the 95% confidence intervals of the differences between any two groups of bootstrap replicates of the exponents of TPL obtained from different leaf size measures did not include 0. In other words, the TPL exponents of leaf size measures from the different physical dimensions could be deemed identical. We found that leaf dry weight provides the best fit of TPL and the most reliable estimate of the exponent among the four leaf size measures used in this study, perhaps because it is the best representative of the energy allocated to individual leaves.

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https://doi.org/10.1016/j.gecco.2019.e00657

1. Introduction

The mean-variance relationships of many ecological measures (e.g., plant biomass measured at different times, developmental rates of arthropods under different temperatures, population densities of trees in quadrats) follow a power law relationship taking the form

$$\text{variance} = \beta \times \text{mean}^{\alpha} \quad (1)$$

referred to as Taylor's power law (TPL), where β is the normalization constant and α is the scaling exponent, both of which are parameters to be fitted by statistical analysis (Cohen et al., 2016; Shi et al., 2017a,b). Parameter α is of central importance in ecology, especially in explaining the temporal or spatial variation of population densities (Taylor, 1961; Kilpatrick and Ives, 2003; Cohen et al., 2016, 2017a, 2017b). Two questions associated with TPL are: (i) which factors give rise to it, and (ii) why do the estimates of the TPL exponent usually range between 1 and 3. With regard to the first question, Cohen and Xu (2015) demonstrated that TPL could arise from random samples of a skewed frequency distribution, and that the scaling exponent of TPL is proportional to the skewness of the distribution. Using simulations, Xiao et al. (2015) concluded that TPL results from two constraints: the number of individuals and the number of sites. Shi et al. (2016) found that TPL describing the numbers of plants in different quadrats can arise from spatial clustering and that the dispersal abilities of parent plants can significantly affect the numerical value of the TPL exponent for offspring number. Zhao et al. (2019) found that measures based on population skewness, the coefficient of variation and synchrony are effective proximate determinants of the TPL exponent. Overall, the skewness of the distribution of ecological measures is closely associated with TPL.

In general, most studies neglect the goodness of fit of TPL to the data. Curiously however, recent studies have shown that the goodness of fit is closely correlated to the physical dimension (e.g., internode length, cross-sectional area, and dry weight) used to measure the culm size of bamboo and that the data of internode dry weight provided the best fit of TPL (Cheng et al., 2017; Liu et al., 2019). Considering that dry weight is representative of energy allocation, Shi et al. (2019a) examined the energy released during earthquake aftershocks in different temporal blocks and showed that the data follow TPL. These authors suggested that TPL appears to be a direct reflection of energy distributions such that different measures of energy obtain the best fit for data complying with TPL.

The goal of this paper was to examine the measures of biological size of differing dimensionality to determine which provides the best fit to data complying with TPL. For this purpose, we examined the leaves of bamboo. Bamboo was selected for study because the leaf shape across 1400 species is astonishingly similar (Bamboo Phylogeny Group, 2012; Shi et al., 2015, 2018; Lin et al., 2016, 2018). In addition, the scaling relationship between leaf weight (arguably a three-dimensional variable, which we label 3D) and leaf area (a two-dimensional variable, 2D) for individual bamboo species is statistically robust, and holds for the pooled data of different species (Shi et al., 2015; Lin et al., 2018; Huang et al., 2019). Although leaf dry weight and fresh weight have the same physical dimension, the water content in a leaf may lead to an inaccurate measure of leaf biomass. We hypothesized that the order of fit among different measures of leaf size would decrease according to the series "leaf dry weight (3D) > leaf fresh weight (3D) > leaf area (2D) > leaf length (1D)". We also examined whether there are significant differences in the estimates of the TPL exponent among these four measures of leaf size.

2. Materials and methods

2.1. Materials

Leaves of 101 bamboo species, varieties, forms, and cultivars were randomly collected from plants mostly growing on the Nanjing Forestry University campus and the White Horse experimental station of Nanjing Forestry University, Nanjing, Jiangsu Province, P.R. China, from May to July of 2018. Between 90 and 110 leaves of each type of plant were sampled from five to twenty healthy adult plants. The collection information is listed in Table S1 of the online supplementary data. After fresh leaves were collected, they were wrapped in wet newspapers and placed into plastic self-sealing bags (28 cm × 20 cm). The leaf fresh weight was subsequently measured in the laboratory using an electric balance (Type: ML 204; Mettler Toledo Company, Zurich, Switzerland; measurement accuracy is 0.0001 g) after wiping them dry with paper tissues. The surface area of each leaf was determined using a scanner (Type: Aficio MP 7502; Rocoh, Tokyo, Japan) to obtain images in bitmap format at a 200-dpi resolution. The methods in Shi et al. (2018) were used to measure leaf length and area. Leaf length was defined as the distance from leaf apex to leaf base. To determine leaf dry weight, leaves were placed in Kraft paper envelopes (33 cm × 24 cm) and into an oven (Type: XMTD-8222; Jinghong Experimental Equipment Co., Ltd., Shanghai, P.R. China) at 105 °C for 2 h and then continuously at 80 °C until achieving constant weight. The basic statistical information for each leaf size measure (including median, mean, standard deviation, skewness and sample size for each investigated species) is provided in Table S2 of the online supplementary data.

2.2. Methods

The mean and variance of leaf length, area, fresh weigh and dry weight was determined from the 90–100 leaves sampled from each type of plant, and a log-log linear model was used to fit the TPL relationship between the mean and variance of each measure, i.e.,

$$\ln(\text{variance}) = \ln(\beta) + \alpha \ln(\text{mean}) \quad (2)$$

Ordinary least-squares was used to estimate the parameters and the corresponding 95% confidence intervals (CIs) of the slope (i.e., α, the scaling exponent of TPL). To examine whether a linear regression was suitable for the data, we determined the following: (i) whether the slope of the above linear regression is significantly different from zero ($P < 0.05$), (ii) the normality of the residuals from the linear regression based on the Shapiro-Wilk test; (iii) the homoscedasticity for the absolute residuals of the linear regression vs. ln(mean), which was considered to be rejected if there is a significant linear relationship ($P < 0.05$) between absolute residuals and ln(mean); and (iv) the linearity for the log-transformed data of variance vs. mean (of any leaf size measure), which was considered to be rejected if the coefficient of $\ln(\text{mean})^2$ of a quadratic model was significant [see Zhao et al. (2019) for details]. The coefficient of determination (namely r^2) was used to measure the goodness of fit of a linear regression.

To test the significance of differences in the estimates of the TPL exponent among the four measures, the bootstrap percentile method (Efron and Tibshirani, 1993; Sandhu et al., 2011) was used. The observations of the mean and variance for each measure were sampled with replacement, and a linear model was used to estimate the slope of TPL of the sampling data. After obtaining 5000 estimates of the TPL scaling exponent, we examined whether the 95% CI of the pairwise differences (from quantile 0.025 to quantile 0.975) in the estimate of the TPL exponent between any two measures included zero. A 95% CI including zero implies that there is no significant difference between two measures; otherwise, the difference is considered to be significant. R software (version 3.2.2; R Core Team, 2015) was used to carry out all calculations.

3. Results and discussion

Significant mean-variance TPL relationships for each of the four leaf size measures were observed (Fig. 1). The data for the mean-variance TPL relationship for leaf length, a one-dimensional physical measure, exhibited the poorest goodness of fit among the four leaf size measures (Fig. 1). However, the exponent was statistically significant and the residuals passed the normality test, which was also true of the other three measures. There is no significant difference in the estimate of the TPL exponent among the four measures (Figs. 1 and 2), although the 95% CI of the TPL exponent of leaf length is broader than that of the other measures. In the case of the two-dimensional (i.e., leaf area) and higher dimensional measures (i.e., fresh weight and dry weight), respectively, the estimates of the TPL exponent were numerically greater than 2, even for the lower bound of the 95% CIs. We interpret this to mean that the extent of variation (as reflected by the coefficient of variation $= \sqrt{\text{variance}}/\text{mean} \times 100\%$) increases with increasing values of the mean. Fig. 1 shows the order of the coefficients of determination for the four measures, which supports the hypothesis that the goodness of fit conforms to the series leaf dry weight > fresh weight > area > length.

The exponents of TPL from different leaf size measures are numerically similar such that each reflects the functional traits of bamboo leaves. The scaling relationship between leaf dry weight and leaf area has been confirmed for many plants (Milla and Reich, 2007; Niklas et al., 2007). Most estimates of the scaling exponent of leaf dry weight vs. leaf area are demonstrably slightly greater than one (Niklas et al., 2007), including bamboo leaves (Shi et al., 2015; Sun et al., 2017; Lin et al., 2018). However, the pooled data for leaf weight vs. area for different bamboo species exhibited a tighter fit than for other groupings (Lin et al., 2018). Based on the pooled data of leaf fresh and dry weights of 5 bamboo species, Huang et al. (2019) found that the estimate of the scaling exponent of leaf dry weight to fresh weight (whose estimate was equal to 1.009 with 95% CI = (1.003, 1.015)) approaches one, which indicates that increases in leaf dry weight approximately keep pace with increases in leaf fresh weight. In summary, the scaling relationship of any two leaf size measures (e.g., leaf area, and fresh and dry weight) is strong. As a result, leaf area and fresh or dry weight all provide good representatives of the energy allocated to leaf construction, which helps to explain why the estimates of the TPL exponent for all three measures of leaf size show no significant difference and the TPL coefficients of determination are so robust (Fig. 1).

Despite that fact that leaf length manifested the poorest fit to TPL, the Montgomery equation has nevertheless been shown to adequately depict the leaf shapes of many herbaceous and woody plants, including bamboo leaves (Montgomery, 1911; Shi et al., 2019b, 2019c). This equation takes the form $A = k\,LW$, where A, L, and W are leaf area, length, and width, respectively, and k is a parameter to be fitted. When the variation of L with respect to W is small, A becomes approximately proportional to L^2. If so, leaf length provides a good representative of leaf area, and should result in little observable difference in the estimates of the TPL exponents between leaf area and leaf length. However, the coefficients of variation of the leaf width/length ratio for different bamboo species range between 8% and 20%, which results in weak leaf area vs. length scaling relationships (Shi et al., 2018, 2019b). This in turn can lead to the lowest estimate of the TPL exponent using the measure of leaf length (Fig. 1a).

There are fierce debates on whether the exponent of TPL is influenced by biotic or abiotic factors (see Xiao et al., 2015, and references therein). Although the skewness of the distribution of measures that generate a TPL can play an important role in determining the TPL exponent (Cohen and Xu, 2015; Zhao et al., 2019), the skewness itself may reflect a universal energy

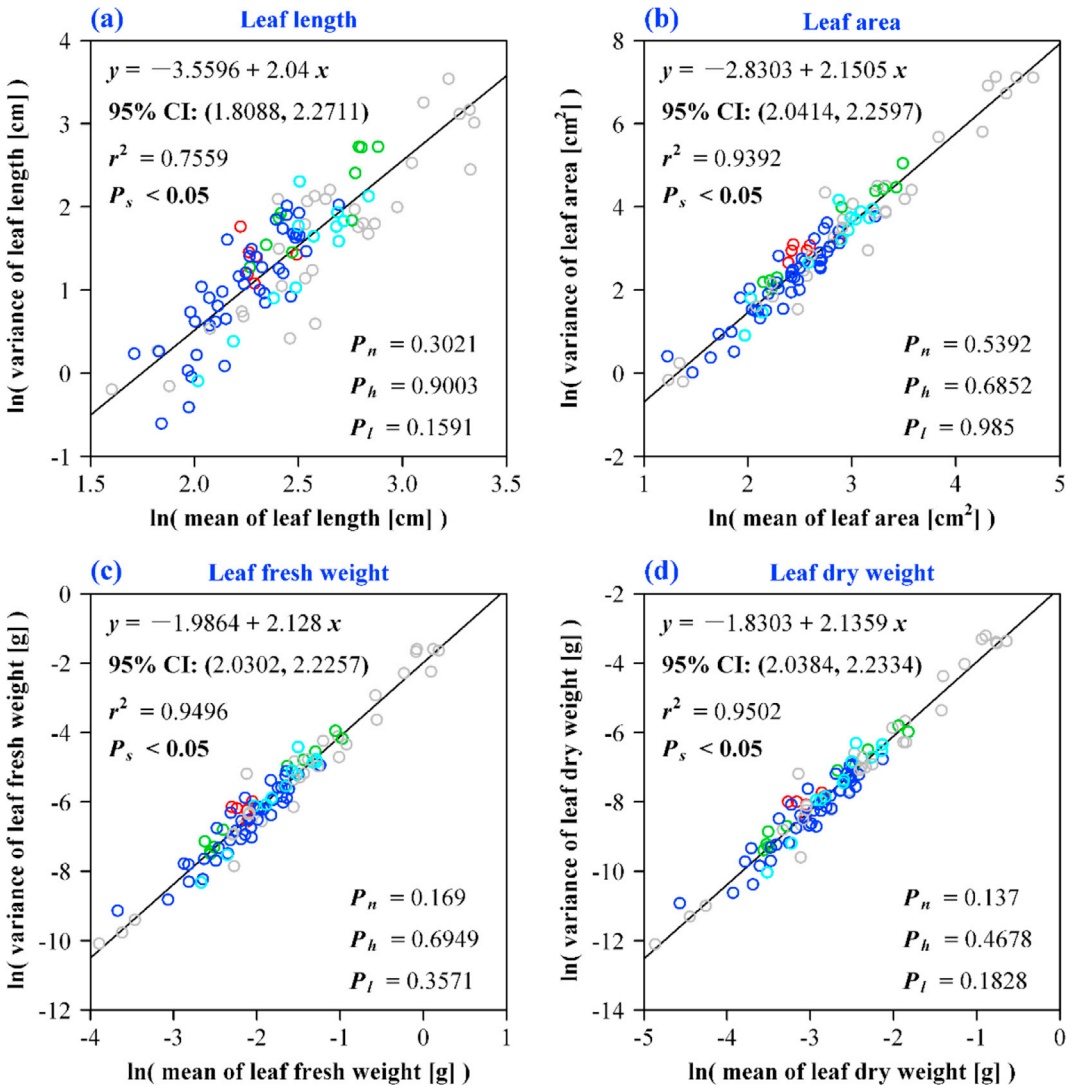

Fig. 1. Taylor's power law (TPL) of four leaf size measures. (a) leaf length, (b) leaf area, (c) leaf fresh weight, and (d) leaf dry weight. $y = \ln(\text{variance})$; $x = \ln(\text{mean})$; 95% CI represents the 95% confidence interval of the slope; the coefficient of determination, r^2, represents the goodness of fit for the linear regression; P_s denotes the result of the significance test for the slope of a log-log linear regression; P_n denotes the result of the Shapiro-Wilk normality test for the residuals; P_h denotes the result of homoscedasticity test for the linear relationship of absolute residuals vs. ln(mean); P_l denotes the result of the linearity of data compared with the quadratic model. The solid line represents the fitted linear regression line; the blue open circles represent the observations of 42 *Phyllostachys* species, varieties, forms, and cultivars; the red open circles represent the observations of 6 *Bambusa* species; the green open circles represent the observations of 10 *Chimonobambusa* species; the light blue open circles represent the observations of 12 *Pleioblastus* species; and the gray open circles represent the observations of the remaining species of genera having less than five species. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

allocation pattern to individuals (Shi et al., 2017b). Thus, we hypothesized that measures that more directly represent energy allocation among individuals should generate stronger TPL scaling relationships between the mean and variance of this measure (Shi et al., 2016, 2017b). Wang et al. (2018) studied the mean-variance relationship of leaf bilateral symmetry (defined as the absolute value of the areal difference between the left and right sub-regions of the leaf lamina), and detected TPLs for different plant taxa. Whether the TPL is strong or weak for a particular species primarily depends on the fit of the scaling relationship between leaf weight and area (Wang et al., 2018; Shi and Liu, 2019). It is apparent that leaf area can be deemed to be a simplified indicator of the energy allocated to a leaf due to the strong scaling relationship between leaf biomass vs. area (Milla and Reich, 2007; Niklas et al., 2007). However, leaf shape could have an important influence on the scaling relationship of leaf weight vs. area. If leaf shape exhibits a large variation within a species, the goodness of fit of the intraspecific data might be low. However, among the more than 1400 species of bamboo, leaf shape can be described by the simplified two-parameter Gielis equation, and both parameters of this equation are a function of leaf width and length (Shi

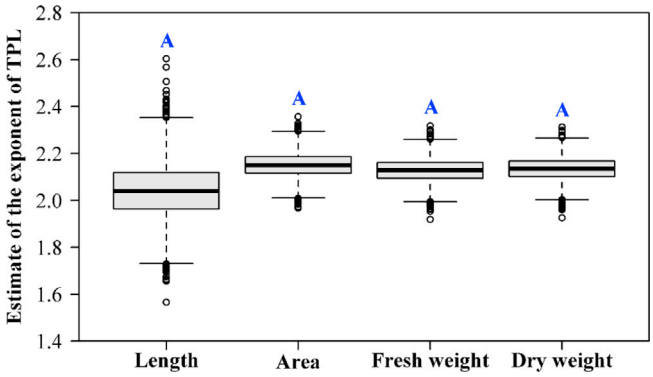

Fig. 2. Boxplots of the estimates of the exponent of Taylor's power law (TPL) for four leaf size measures. The values forming the box were calculated using 5000 bootstrap replications. The letters above the boxes are used to exhibit significant differences between pair of plants at the significance level of 0.05. Measures sharing the same letter indicate no significant difference; otherwise, there is a significant difference.

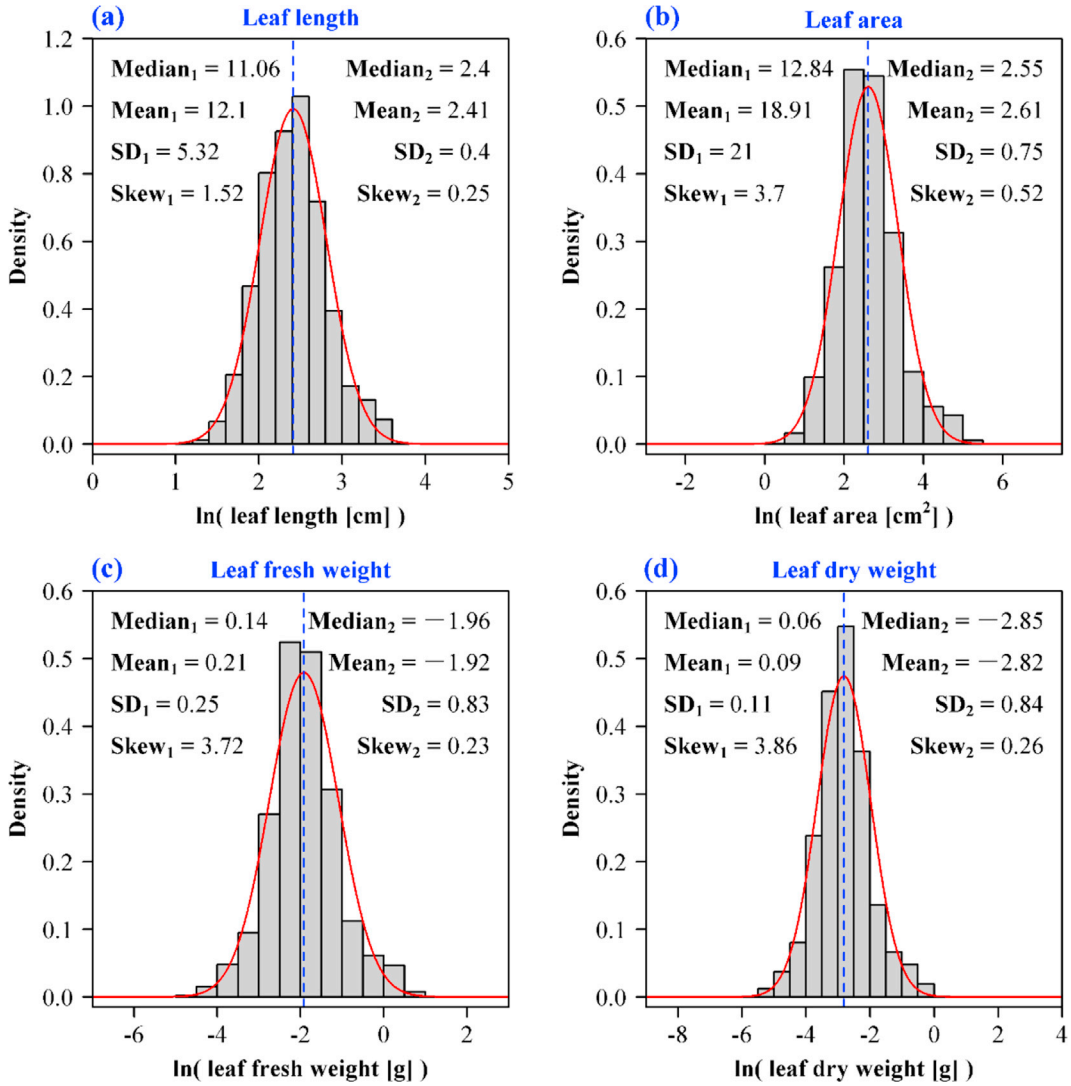

Fig. 3. Distributions of the log-transformed values for four leaf size measures. In each panel, the red bell-shaped curve represents the normal distribution; the gray histogram was formed by observations; $Median_1$, $Mean_1$, SD_1 and $Skew_1$ represent the median, mean, standard deviation and skewness of leaf size measure before the log-transformation, whereas $Median_2$, $Mean_2$, SD_2 and $Skew_2$ represent the median, mean, standard deviation and skewness of the log-transformed leaf size measure. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

et al., 2015, 2018). Thus, the leaf shape of bamboos appears to be highly conserved, thereby providing a good fit of TPL between the mean and variance for the interspecific pooled data (Fig. 1b, c, and d).

Cohen and Xu (2015) demonstrated that observations randomly sampled in blocks from any single skewed frequency distribution with four finite moments could result in TPL because the covariance of the sample mean and the sample variance is proportional to the skewness of the underlying distribution. After pooling the data of each leaf size measure (= 10,045 data points), we used the beta, exponential, Gamma, log-normal and Weibull distributions based on the R special package "bbmle" (version 1.0.18) (Bolker, 2008) to fit the data, and subsequently used a two-sample Kolmogorov-Smirnov test (Conover, 1971) using the "ks.test" function in R (version 3.2.2) to examine the significance of each distribution. However, all distributions did not pass the Kolmogorov-Smirnov test (five p-values < 0.05) for each leaf size measure probably because the sample sizes are extremely large. In general, very large samples especially over 10,000 cause p-values to rapidly approach zero, which might mislead investigators to conclude the data are not statistically significant (Lin et al., 2013). Thus, we used the R special package "EnvStats" (version 2.3.1) to draw the Quantile-Quantile (Q-Q) plots (i.e., sample quantiles vs. theoretical quantiles of each leaf size measure). We found that for the log-normal distribution the data of sample quantiles vs. theoretical quantiles fit the straight line model $y = x$ better than the others (not shown because of limited space). In this case, we believe that the log-normal distribution could describe the distribution features of these leaf size measures. Fig. 3 shows the comparison of the median, mean, standard error and skewness before the log-transformation of each leaf size measure with those after the log-transformation of its measure. We find that after the log-transformation the sample distribution is approximately normal. In addition, the absolute value of the skewness becomes smaller and approaches zero, which also provides evidence that the log-normal distribution is appropriate (Fig. 3).

4. Conclusions

We have shown that four different measures of leaf size (leaf length, area, and fresh and dry weight) follow TPL using pooled data from 101 species, varieties, forms, and cultivars of bamboo. We have also shown that the TPL scaling exponent of leaf length and those of another three leaf size measures are not significantly different. Among the four measures, the mean and variance of dry weight exhibited the strongest TPL, while the TPL of leaf length showed the weakest, i.e. with increasing leaf size dimensionality, the corresponding TPL becomes stronger. We also examined and found support for the hypothesis that TPL variance vs. mean relationships of leaf size measurements reflect the energy allocation to individual leaves, and might thus manifest the same (or numerically similar) power exponents. Although leaf number and size differ greatly among bamboo species, varieties, forms, and cultivars, the tight fit of TPLs suggests that the variation of leaf size can be accurately estimated knowing its mean.

Acknowledgements

We thank Xiao Zheng, Jialu Su, Yawen Wan, Yayun Yang, Lijuan Shao, Yu Zhang, Fang Li, and Huajun Fu for their valuable work in collecting leaves. P. Shi was supported the Priority Academic Program Development of Jiangsu Higher Education Institutions; S. Lin was supported by the National Natural Science Foundation of China (grant number 31870595).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00657.

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